

# Historical demography of *Lantana camara* L. reveals clues about the influence of land use and weather in the management of this widespread invasive species



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## Abstract

Weather is a general stochastic influence on the life history of weeds. In contrast, anthropogenic disturbance (e.g. land use) is an important deterministic influence on weed demography. Our aim with this study was to investigate the relative contributions of land use and weather on the demography of *Lantana camara* (lantana), a weed of agricultural and natural habitats, based on the intensive monitoring of lantana populations under three land uses (viz. farm[pasture], and burnt and grazed forests) in subtropical Australia. Lantana populations were growing vigorously across all land uses (asymptotic population growth rate,  $\lambda > 3$ ). Examination of historical demography using retrospective perturbation analyses showed that weather was a strong influence on lantana demography with the transition from an El Niño (2008–09) to a La Niña (2009–10) year having a strong positive effect on population growth rate. This effect was most marked at the grazed site, and to a lesser extent at the burnt site, with seedling-to-juvenile and juvenile-to-adult transitions contributing most to these effects. This is likely the result of burning and grazing having eliminated/reduced interspecific competition at these sites. Prospective perturbation analyses revealed that  $\lambda$  was most sensitive to proportionate changes in growth transitions, followed by fecundity and survival transitions. Examination of context-specific patterns in elasticity revealed that growth and fecundity transitions are likely to be the more critical vital rates to reduce  $\lambda$  in wet years at the burnt and grazed forest sites, compared to the farm/pasture site. Management of lantana may need to limit the transition of juveniles into the adult stages, especially in sites where lantana is free from competition (e.g. in the presence of fire or grazing), and this particularly needs to be achieved in wet years. Collectively, these results shed light on aspects of spatial and temporal variation in the demography of lantana, and offer insights on its context-specific management.

## Zusammenfassung

Das Wetter ist ein allgemeiner stochastischer Einflussfaktor für die Lebensgeschichte von Unkräutern. Im Gegensatz dazu ist anthropogene Störung (z.B. Landnutzung) ein wichtiger determinierender Einfluss auf die Demographie von Unkräutern. Das Ziel unserer Studie war es, die relativen Beiträge von Landnutzung und Wetter zur Demographie von *Lantana camara* (Lantana) zu untersuchen, einem Unkraut, das in landwirtschaftlichen und naturnahen Habitaten vorkommt. Die Grundlage bildete ein intensives Monitoring von Lantana-Populationen im subtropischen Australien, wobei drei Landnutzungsarten

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untersucht wurden, namentlich Landwirtschaft (Heuwiesen) sowie Wald unter Feuer- bzw. Beweidungseinfluss. Die *Lantana*-Populationen wuchsen kräftig unter allen Landnutzungsbedingungen (asymptotische Populationswachstumsrate:  $\lambda > 3$ ). Die Untersuchung der historischen Demographie mit retrospektiven Perturbationsanalysen zeigte, dass das Wetter ein starker Einflussfaktor für die Demographie von *Lantana* war, wobei der Übergang von einem El Niño- (2008–09) zu einem La Niña-Jahr (2009–10) einen stark positiven Effekt auf die Populationswachstumsrate hatte. Dieser Effekt war besonders markant auf der beweideten Fläche und –in geringerem Ausmaß– auf der Feuerfläche, wobei die Übergänge vom Sämling zur Jungpflanze und von der Jungpflanze zur adulten Pflanze am meisten beitrugen. Dies ist vermutlich darauf zurückzuführen, dass Feuer und Beweidung die interspezifische Konkurrenz auf diesen Flächen eliminiert oder reduziert hatten. Prospektive Perturbationsanalysen zeigten, dass  $\lambda$  äußerst empfindlich gegen anteilmäßige Veränderungen bei den Wachstumsübergängen war, gefolgt von Fekundität und populationsdynamischen Übergängen. Die Untersuchung von kontextspezifischen Elastizitätsmustern zeigte, dass Wachstums- und Fekunditätsübergänge vermutlich wichtigere Vitalraten für die Reduktion von  $\lambda$  in feuchten Jahren auf den von Feuer bzw. Beweidung beeinflussten Waldflächen waren als auf der Mähwiesenfläche. Zusammengefasst werfen diese Ergebnisse ein Licht auf die räumliche und zeitliche Variation in der Demographie von *Lantana*, und sie erlauben Schlüsse für ein kontextspezifisches Management. Das Management von *Lantana* könnte die Begrenzung des Überganges von den Jungpflanzen zu den adulten Stadien erfordern, insbesondere auf Flächen, auf denen *Lantana* ohne Konkurrenz wächst (Feuer, Beweidung), und dies muss insbesondere in feuchten Jahren erreicht werden.

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**Keywords:** *Lantana camara*; Life-table response experiment (LTRE); Elasticity; Vital rates; Fire; Grazing; Pasture; Matrix population models

## Introduction

Widespread weeds pose significant challenges to management. Their success is often the result of a combination of innate demographic characteristics and their ability to take advantage of a broad range of biotic and abiotic environmental conditions (Mitchell et al. 2006; Sheppard, Alexander, & Billeter 2012). Understanding the relative importance of these factors is necessary to formulate context-specific management tactics for such plants (Hobbs & Humphries 1995). Syntheses of demography have offered valuable insights into potentially general approaches to the management of weeds based on the structure of weed life history (Silvertown, Franco, Pisanty, & Mendoza 1993; Franco & Silvertown 2004; Ramula, Knight, Burns, & Buckley 2008). Increasingly, the biotic (e.g. herbivory, competition) and abiotic (e.g. cropping system, edaphic factors, microclimate) environmental contexts that serve as the theaters for plant demography are being examined for their influences on the success and impacts of weeds (McEvoy & Coombs 1999; Davis, Dixon, & Liebman 2003; Shea, Kelly, Sheppard, & Woodburn 2005; Mitchell et al. 2006; Wortman et al. 2012).

Weather and disturbance are important factors affecting the invasiveness of weeds (Hobbs & Humphries 1995; Catford et al. 2012; Murray, Stokes, & van Klinken 2012). While climate sets the broad bounds of favorability of conditions for the distribution of weeds, near-term weather is a general stochastic influence on their life history. The ability of weeds to respond rapidly to prevailing weather conditions is an important factor contributing to their invasiveness (e.g. Sheppard et al. 2012). The timing of management of weeds in relation to weather is therefore important. While natural disturbance (e.g. extreme weather events) is

a stochastic influence on the distribution and abundance of weeds, anthropogenic disturbance (e.g. land use) is an important deterministic influence on invasive weeds (Hobbs & Humphries 1995; Catford et al. 2012). Understanding how weeds perform in relation to land use is therefore important in developing methods to manage them through the alteration of land use and/or the development of context-specific management options. Elucidating such influences of the interplay of weather and land use on the invasiveness of the widespread weed *Lantana camara* L. (Verbenaceae; *lantana* hereafter) is the objective of this study.

*Lantana* is a perennial plant of neotropical origin that was spread globally through the ornamental-plant/nursery trade (Swarbrick, Wilson, & Hannan-Jones 1995). It has subsequently become an invasive weed of rangelands and natural areas in Africa, Asia and Australia (Day, Wiley, Playford, & Zalucki 2003; Bhagwat, Breman, Thekaekara, Thornton, & Willis 2012). *Lantana* impacts pasture productivity through alteration of soil physicochemical properties, outcompeting/suppressing palatable grasses, alteration of fire regimes, and through the formation of thickets impeding movement of livestock (Gentle & Duggin 1997a, 1997b; Duggin & Gentle 1998; Osunkoya & Perrett 2011; Vardien et al. 2012). Its impacts on natural areas are equally severe. These include negative impacts on richness and diversity of native plant species across multiple structural groups, and associated decline in habitat quality for birds and mammals (Gooden, French, & Turner 2009; Gooden, French, Turner, & Downey 2009; Vardien et al. 2012). As a result, *lantana* is regarded among the most significant invasive weeds globally and has been the target for intensive management efforts for over a century (Day et al. 2003; Zalucki, Day, & Playford 2007; Bhagwat et al. 2012). More recently, greater effort is

being placed on directing management actions based on a thorough understanding of lantana life history and demography (Osunkoya, Perrett, & Fernando 2010; Osunkoya, Perrett, Fernando, Clark, & Raghu 2012; Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). This study is part of this broader effort.

We addressed the following questions, based on intensive studies of lantana across three sites in subtropical Australia: (1) How do differences in land use and weather influence the demography of lantana? (2) What life cycle transitions were responsible for the apparent differences in lantana demography across sites with differing land use? (3) How might insights gleaned from examining past demography of lantana be combined with information from prospective analyses of its life history, and facilitate better management of this invasive weed in different land use contexts?

## Materials and methods

### Study sites and data collection

The study was done in southeastern Queensland, Australia, ca. 200 km north west of Brisbane near the towns of Yarraman and Blackbutt (26°50′–26°54′S; 151°56′–152°02′E). Details of the study region (including, climate and land use history of specific sites) are presented in related publications (Osunkoya & Perrett 2011; Osunkoya et al. 2012; Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). Important aspects of the site history pertaining to this paper are outlined here. Land use in this region is a mixture of cropping, pasture and forestry. The sites used for this study were under a mixture of land uses, specifically hay pasture ('Farm' hereafter), and managed forestry. The forested sites were open eucalypt forest that either had the presence of cattle grazing ('Grazed' hereafter) or experienced fire ('Burnt' hereafter) to suppress the ground layer vegetation, especially lantana growth and spread, with a low-intensity burning regime typically being applied once every 3 years. Fire was used at the Burnt site toward the end of the austral winter in 2006 and 2009. Lantana infests all of these sites and this enabled the examination of its demography under different land uses. Permanent plots were established in 2008 in each of the three study sites; the size of the plots was 50 m × 50 m, 30 m × 50 m and 50 m × 50 m in the Farm, Burnt and Grazed sites, respectively.

All individual lantana plants were uniquely tagged within each plot in 2008 and their fates were followed in two successive years (2009 and 2010). Over the course of the entire study, the fates of some 2000 individual plants were followed. Following the life-cycle of lantana (Fig. 1), individuals were classified on the basis of their height into seedlings (10–20 cm), juveniles (21–60 cm), small adults (61–100 cm), medium adults (101–160 cm) and large adults (>160 cm). New recruits to the populations and their fates were recorded in 2009 and 2010. In addition, size-specific fecundity was estimated by harvesting fruits from different size classes

of plants adjacent to, but outside, the permanent monitoring plots. Soil seedbank dynamics were also studied at each site by following the fate of bags of buried seed (Osunkoya, Perrett, Fernando, & Clark 2013). From these surveys, six site × year population projection/transition matrices ( $A$ ) were assembled from the three sites with different land uses during each of the two study periods (2008–09 and 2009–10; Table A1 in Appendix A). Elements of the projection matrix ( $a_{ij}$ ) represent the key annual demographic transitions (upper-level vital rates, *sensu* Caswell 2001) in lantana life history (Fig. 1); details of the calculations of the vital rates are presented in Appendix A (Tables A2 and A3) and in related publications (Osunkoya et al. 2010, 2012; Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). Errors detected in compilation of the transition matrix in these earlier studies, specifically concerning the seedbank to the seedling transition and the germination of seeds in the year following their production, have been corrected in this study by incorporating additional information on seed dormancy and seedling recruitment patterns (Vivian-Smith & Panetta 2009; Raizada & Raghubanshi 2010; Osunkoya, Perrett, Fernando, & Clark 2013).

### Weather

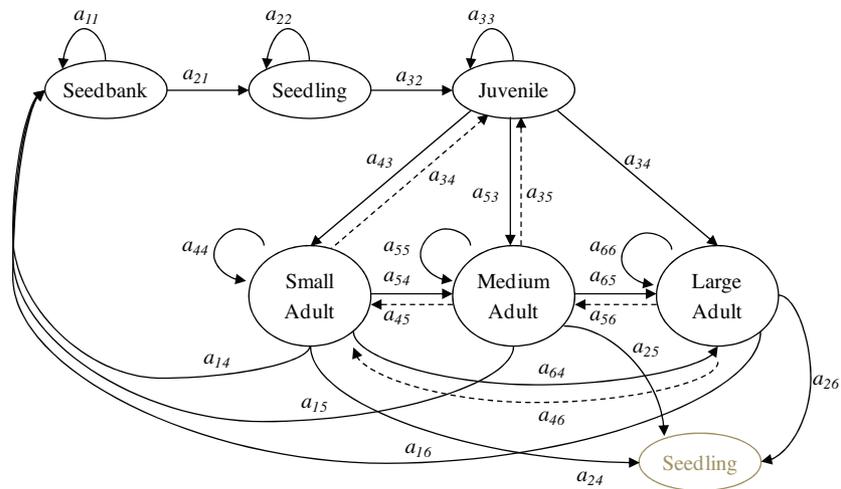
Much of Australia experienced the worst drought on record between 2003 and 2009 as a result of an El Niño weather pattern (Bureau of Meteorology 2012). This drought broke with the onset of a strong La Niña weather pattern in 2009, resulting in the wettest spring on record in 2010 over much of eastern Australia (Bureau of Meteorology 2012). The temporal monitoring of lantana populations in this study fortuitously spanned a significant temporal rainfall gradient from drought to wet weather. Hence the 2008–09 ('2009' hereafter) and 2009–10 ('2010' hereafter) transitions can be thought of as being representative of lantana demography under dry versus wet weather, respectively.

### Data analysis

#### Retrospective perturbation analysis

We used a two-way factorial design life-table response experiment (LTRE) to analytically understand the effect of land use and climate contexts on the weed population growth rates, through their impact on the individual vital rates. The goal of this LTRE analysis is to provide insights on historically important vital rates that may be of interest for future integrated weed management programs for lantana. An LTRE is analogous to an ANOVA, and allows understanding differences in population growth rate ( $\lambda$ ) as a function of land use, time and their interaction, relative to the projected population growth rate of a reference matrix (Caswell 2001; Angert 2006; Eq. (1)), as:

$$\lambda^{(ly)} = \lambda^{(\cdot\cdot)} + \alpha^{(l)} + \beta^{(y)} + \alpha\beta^{ly} \quad (1)$$



**Fig. 1.** Life cycle graph indicating life stages (seedbank) and height-classes (seedlings (10–20 cm), juveniles (21–60 cm), small adults (61–100 cm), medium adults (101–160 cm) and large adults (>160 cm)) of *Lantana camara*. Annual transitions are indicated by arrows; self-loops indicate survival, solid arrows from the adult classes to the seedbank/seedling stage indicate fecundity, all other solid arrows indicate growth, and dashed arrows indicate retrogression. Seeds that germinate to become seedlings in the year following their production (i.e. do not remain dormant, as part of the seedbank) are indicated separately in the interest of clarity. Vital rates are indicated in standard matrix notation (*sensu* Caswell 2001).

where  $\alpha^{(l)}$  is the effect of the  $l$ th level of land use,  $\beta^{(y)}$  is the effect of the  $y$ th level of year and  $\alpha\beta^{(ly)}$  is the interaction of the  $l$ th land use and  $y$ th year, measured relative to the projected growth rate of the reference matrix ( $\lambda^{(c)}$ ). Unlike ANOVA, where the coefficients in the model are estimated by least squares, here the sensitivities of  $\lambda$  to perturbation of the vital rates provide those coefficients analytically (Caswell 2001).

We used the average of transition rates across all land uses and times as the reference matrix (Miriti, Wright, & Howe 2001). Treatment matrices for land use ( $A^{(l)}$ ) and year ( $A^{(y)}$ ) were obtained by pooling data across all years for a given land use and across all land uses for a given year respectively. The effects of land use, year and their interaction were examined by evaluating sensitivity  $\partial\lambda/\partial a_{ij}$  midway between the treatment and reference ( $A^{(c)}$ ) matrices (Horvitz, Schemske, & Caswell 1997; Caswell 2001; Angert 2006; see Eqs. (A1)–(A4) in Appendix A).

The contributions of particular transition matrix elements  $a_{ij}$  to variation in  $\lambda$  within the context of land use and year were examined to understand how *lantana* demography was affected at the study sites by land use and time.

### Prospective perturbation (elasticity) analysis

Elasticity (the sensitivity of  $\lambda$  to proportionate change in a given demographic rate) is a valuable metric in understanding the relative contributions of vital rates to overall population growth (Horvitz et al. 1997; Caswell 2000, 2001). The elasticity ( $E_{ij}$ ) of a given transition matrix element ( $a_{ij}$ ) was calculated for each site  $\times$  year matrix as per Eq. (2):

$$E_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial\lambda}{\partial a_{ij}} \quad (2)$$

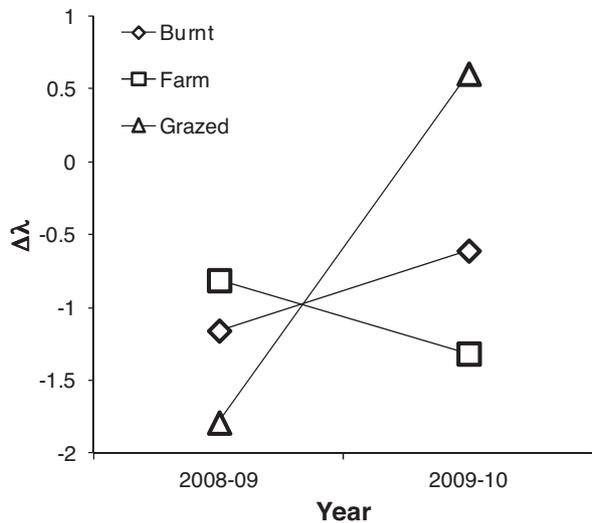
We grouped transition matrix elements into those representing survival (diagonal elements), growth/retrogression (sub-diagonal, supra-diagonal elements [except fecundity elements]) and fecundity (elements of the first and second row from columns representing reproductive classes), and looked at the summed elasticities of these three components of *lantana* life history to gain insight on management approaches for this species in different contexts.

All demographic analyses were done using R v.2.15.3 using the package ‘popbio’ (Stubben & Milligan 2007; R Core Team 2012). All scripts used for analyses are provided as online supplementary material.

## Results and discussion

### Retrospective perturbation analysis (LTRE)

*Lantana* populations grew vigorously across all land uses in both wet and dry years (asymptotic population growth rate ( $\lambda$ ):  $\lambda_{\text{Farm}}^{2009} = 4.56$ ;  $\lambda_{\text{Farm}}^{2010} = 4.07$ ;  $\lambda_{\text{Burnt}}^{2009} = 4.22$ ;  $\lambda_{\text{Burnt}}^{2010} = 4.77$ ;  $\lambda_{\text{Grazed}}^{2009} = 3.59$ ;  $\lambda_{\text{Grazed}}^{2010} = 5.99$ ). Diagnosis of *lantana* populations using an LTRE revealed valuable insights into its historical demography. In general, land use at each site had a net negative contribution to the deviation of  $\lambda$  (Figs. 2 and 3A) from the reference matrix, while year’s contribution was negative in 2009 and positive in 2010 (Figs. 2 and 3B). At the Farm and Burnt sites, deviation of population growth rate of *lantana* relative to the reference matrix was consistent over time (Figs. 2 and 3C). This was in contrast to *lantana* population dynamics at the Grazed site where the population growth rate was substantially lower than that indicated by the reference matrix in 2009, but was greater than that in the



**Fig. 2.** Deviation of population growth rate ( $\Delta\lambda$ ) of *Lantana camara* at sites with different land uses ( $\lambda^{(by)}$ ), with reference to the population growth rate of the pooled reference matrix ( $\lambda^{(c)}$ ) ( $\Delta\lambda = \lambda^{(by)} - \lambda^{(c)}$ ).

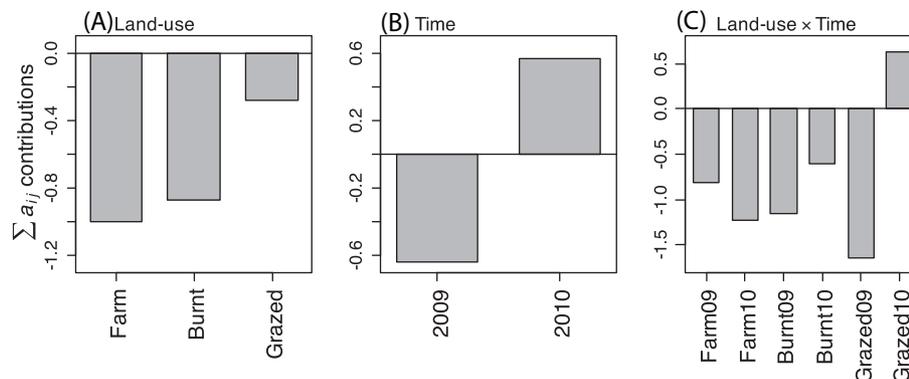
reference matrix in 2010 (Fig. 3C). This temporal difference across the sites suggested a significant land use  $\times$  time interaction effect (Fig. 2). As in the case of an ANOVA, the main effects of LTRE factors cannot be interpreted independent of each other in the presence of interaction effects.

Examination of the contributions of vital rates to the observed differences in lambda ( $\Delta\lambda$ ) reveals important differences in lantana demography in relation to land use and year. In terms of the magnitude of the contributions, transitions into the medium adult and seedling stages had the largest contribution to deviation of  $\lambda$ , followed by those into juveniles, small adults and large adults (Fig. 4). In general terms, seedbank appeared to have the lowest contributions across all land use  $\times$  time combinations (Fig. 4A). Across both annual transitions, contributions of seedlings from non-dormant seeds produced by all three adult classes ( $a_{24}$ ,  $a_{25}$ ,

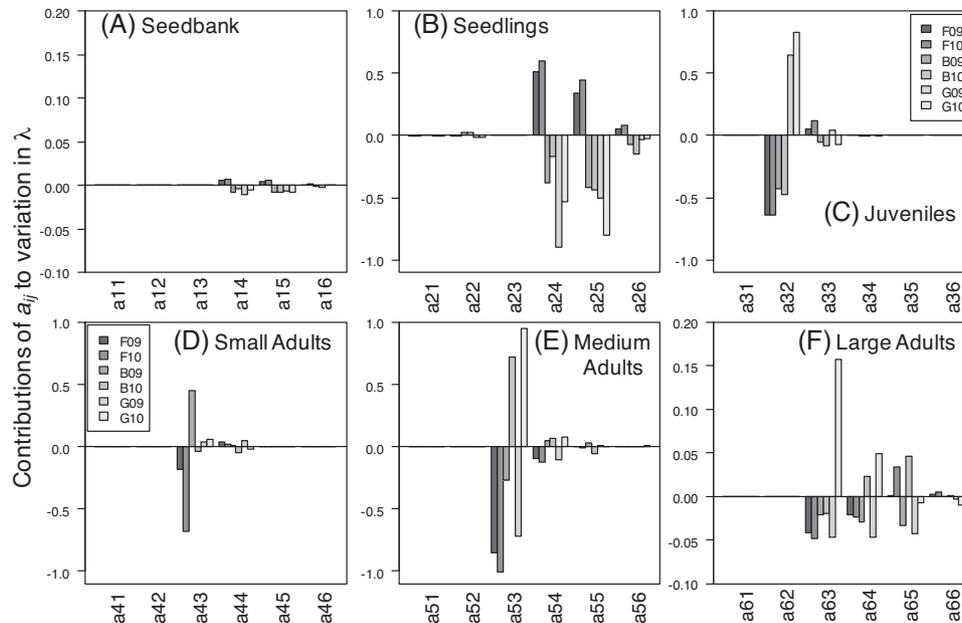
$a_{26}$ ) were positive in the Farm site while they were negative in the Burnt and Grazed sites (Fig. 4B). The contributions of large adults to these differences were lower than those of the small and medium adults (Fig. 4B). Across both years, growth of seedlings into juveniles ( $a_{32}$ ) had a positive contribution to  $\lambda$  in the Grazed site, and a negative contribution in the other two land use types (Fig. 4C). In contrast, juvenile survival ( $a_{33}$ ) had a small positive contribution to  $\lambda$  in the Farm site in both years and the Grazed site in 2009, but a negative contribution across other land use  $\times$  year combinations (Fig. 4C). Growth of juveniles into small adults ( $a_{43}$ ) had a negative contribution to  $\lambda$  at the Farm in both years, while it had a positive contribution in the Burnt site in 2009 (Fig. 4D). The transition of juveniles into medium adults ( $a_{53}$ ) in 2010 at both the Burnt and Grazed sites had a large positive contribution to  $\lambda$ , while it had large negative contributions across other land use  $\times$  year combinations (Fig. 4E). Transitions into the large adult class, and the survival of large adults in general had small contributions to  $\lambda$ ; the most noteworthy among these was the relatively large positive contribution of the transition of juveniles to large adults ( $a_{63}$ ) in the Grazed site in 2010 (Fig. 4F).

The main effects of land use and time are presented as part of the supplementary online information (Figs. A1 and A2 in Appendix A).

Consistent with the known biology of lantana (Carrión-Tacuri, Rubio-Casal, de Cires, Figueroa, & Castillo 2011), when light is not limiting (e.g. at the Farm site) reproductive output (specifically in the form of recruitment of seedlings from non-dormant seeds produced in the previous year) contributes strongly to the weed's demography irrespective of rainfall (Fig. 4B). Seeds of lantana are known to respond to smoke (Raizada & Raghubanshi 2010), and the consistency of seedling recruitment's positive (albeit relatively small) contribution to population growth rate across dry and wet years in the burnt site, bears this out under the field conditions of this study (Fig. 4B). However, this benefit to recruitment as a result of fire does not appear to translate into positive demographic contributions of the seedling-to-juvenile



**Fig. 3.** Contributions of (A) land use, (B) time and (C) their interaction to the deviation of population growth rate ( $\Delta\lambda$ ), with reference to the population growth rate of a pooled reference matrix, as revealed by an LTRE on the demography of *Lantana camara* in southeastern Queensland, Australia. Contributions are the summed contributions of the vital rates ( $a_{ij}$ ).



**Fig. 4.** The contributions of transition matrix elements ( $a_{ij}$ ) to spatiotemporal variation of population growth rate of *Lantana camara* in southeastern Queensland, Australia. The matrix elements are grouped by transitions to the (A) seedbank and height-classes: (B) seedling (10–20 cm), (C) juveniles (21–60 cm), (D) small adults (61–100 cm), (E) medium adults (101–160 cm) and (F) large adults (>160 cm). Please note differences in y-axis scale.

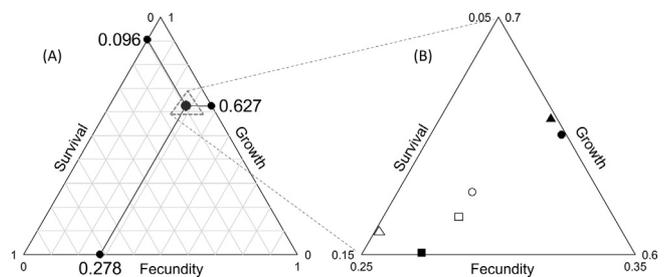
transition ( $a_{32}$ ; Fig. 4C); in contrast to the Burnt site, this transition had a consistently positive and strong contribution to  $\lambda$  in the Grazed site (Fig. 4C). The observed difference in the contribution of the seedling-to-juvenile transition ( $a_{32}$ ) between the Burnt and Grazed sites is presumably because of reduced competition from palatable grasses as a result of grazing, while burning negatively impacts lantana as much as its competitors (Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). With the onset of wet weather in 2010 the transition of juveniles into small adults ( $a_{43}$ ) negatively affected demography at the Farm site; whereas under the drought conditions of 2009 this transition had a positive effect on demography at the Burnt site (Fig. 4D). Wet weather resulted in the juvenile-to-medium adult transition ( $a_{53}$ ) having a strongly positive influence on demography at both the Burnt and Grazed sites (Fig. 4E). This is likely the result of burning and grazing having reduced/eliminated interspecific competition at these sites, enabling juvenile lantana to grow into reproductive adults in the absence of competition and the return of favorable weather conditions.

### Prospective perturbation (elasticity) analysis

Elasticity analyses enable us to identify targets for management intervention in the life cycle of lantana to suppress its populations (Caswell 2000). Averaged across all land use  $\times$  time interactions, the summed contributions of vital rates revealed that  $\lambda$  was most sensitive to proportionate changes in growth transitions, followed by fecundity and survival transitions (Fig. 5A). Examination of context-specific

patterns in elasticity revealed that growth and fecundity transitions are likely to increase their influence on  $\lambda$  in wet years at the Burnt and Grazed sites (Fig. 5B). This effect was not as pronounced at the Farm site.

The analyses above partly conform with the general management guidelines of Ramula et al. (2008), that recommend focusing primarily on survival and growth transitions for long-lived (>12 years) weeds, but concur with recent analyses that growth transitions should be primary targets for lantana management in general (Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). Teasing apart of the influence of land use and weather suggests that managing growth is particularly important in Burnt and Grazed sites in wet years



**Fig. 5.** Triangular ordination showing (A) the overall mean of the summed elasticities for survival, growth and fecundity vital rates, and (B) the summed elasticities for survival, growth and fecundity vital rates for three populations of *Lantana camara* growing under different land-use scenarios (square: Farm; circle: Burnt; triangle: Grazed), across 2 years (open symbol: 2009; filled symbol: 2010), in southeastern Queensland, Australia. The triangular region in (A) with the dashed lines is the elasticity space plotted in (B).

(Fig. 5B). Our related work has shown that seedbank-to-seedling, seedling-to-juvenile and juvenile-to-small adults transitions are important management targets in Farm sites. The first two of the aforementioned transitions are important at Grazed and Burnt forest sites as well, but in wet years controlling the rapid growth from juveniles-to-medium adults increases in importance (Osunkoya, Perrett, Fernando, Clark, & Raghu 2013).

Given the widespread nature of lantana's distribution, the costs of chemical and mechanical control and the fact that lantana invades both agricultural and natural lands, current management of lantana is largely focused on the use of specialist insects and pathogens to effect biological control of this weed (Day et al. 2003). Despite the extensive resources expended in this regard, the returns in terms of lantana management have been minimal (Zalucki et al. 2007). This study provides clues on the types of life history impacts that any management action may need to have, in relation to land use and weather, to effectively manage this weed. The extent to which these factors may be interfering with the contributions of biological control to lantana management needs systematic verification (e.g. Shea et al. 2005). For example, in order to be effective, a biological control agent may need to strongly limit the transition of juveniles into the adult stages, especially in sites where lantana is free from competition (e.g. in the presence of fire or grazing), and they particularly need to achieve this in wet years. Besides identifying life history targets for management intervention, this study also highlights the potential role for using competition from co-occurring species in lantana management; managing land use practices such as fire and grazing pressure are likely to be important in this regard (Osunkoya, Perrett, Fernando, Clark, & Raghu 2013). The interaction between the role of plant competition (facilitated by land use) and biological control needs urgent and careful examination for the management of this weed, as has been elegantly done in other systems (McEvoy & Coombs 1999).

To our knowledge, this study is the most intensive demographic investigation tracking the fate of individuals of lantana across its entire life history and across different land use and weather conditions. However, we would like to place two important caveats on making inferences from this work. Though our sites were under different land uses, they are part of the same catchment. While this enables us to make strong inferences on lantana demography in relation to land use at this location, it may not necessarily represent differences in land use across all locations. In addition we opportunistically happened to record transitions spanning the extremes of drought and rain, hence we interpreted our temporal/year effects to be representative of weather. Ideally, despite the logistics and costs of such a study, sampling across multiple catchments and across a longer timeframe would enable a more general inference of land use and weather effects. These caveats notwithstanding, our study sheds light on spatial and temporal variation in the demography of a significant widespread invasive weed of agricultural

and natural habitats, and offers insights on its context-specific management.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2014.08.006>.

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